Zoogeographic provinces of the Humboldt, Benguela and Leeuwin Current systems

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Abstract

The distributional patterns of inshore marine faunas of southern South America, southern Africa and southern Western Australia are discussed. They are related to the effects of the cold northward flowing Humboldt and Benguela Currents and warm southward flowing Leeuwin Current respectively. The extent and nature of zoogeographic provinces, their faunal affinities and levels of endemicity are reviewed. In South America and southern Africa, cold temperate provinces resulting from the effects of the cold currents and associated upwellings act as barriers to dispersal of warm water faunas especially along the southwestern coasts. A corresponding cold temperate province is absent from southwestern Australia and warm water species are distributed farther south than in South America and Africa.

Introduction

Surface current patterns in the Atlantic, Pacific and Indian Oceans are characterized by major gyres that flow along the oceanic boundaries in a clockwise direction in the northern hemisphere and counter-clockwise in the southern hemisphere. The cold water, northward flowing Humboldt and Benguela Currents act with the prevailing winds to produce upwellings of nutrient-rich subsurface waters along the western coasts of southern South America and Africa. The high nutrient levels provide for increased phytoplankton production and so high production by zooplankton and secondary consumers such as anchovies (Tait 1968, Cushing & Walsh 1976).

The presence of a southward flowing current along the western coast of Australia that contacted the Houtman Abrolhos but did not reach the continental mainland was postulated by Saville-Kent (1897). Dakin (1919) compared temperatures at the Houtman Abrolhos with those at Geraldton, providing evidence of a warm offshore current. The presence of tropical species of marine invertebrates, especially molluscs, at the western end of Rottnest Island led marine biologists in the 1950's to conclude that there must be a current bringing planktonic larvae of tropical species south from areas such as the Houtman Abrolhos. It was not until 1980 that the Leeuwin Current was described (Cresswell & Golding 1980).

Current systems have major effects on the distributions of marine biota (Sverdrup *et al.* 1942, Ekman 1953, Briggs 1974, Cushing & Walsh 1976). Currents significantly influence the dispersal of organisms, especially of larval stages. Also, they determine the ambient conditions along much of the inshore environment, particularly with respect to water temperatures, salinity and nutrients. As a result, they permit survival of species in areas that would otherwise be unsuitable. Conversely, they can act as barriers to settlement by distributing organisms away from suitable habitats or by causing otherwise suitable habitats to become sub-optimal or uninhabitable.

The oceanography of the Humboldt, Benguela and Leeuwin Currents is discussed in detail by Pearce (1991) and is only briefly noted here. This paper summarises the effects of these currents on faunal distributions, and hence zoogeographic provinces, of the southern shores of South America, Africa and Australia (Fig.1). The three regions are discussed in turn and subsequently compared. The currents primarily influence southwestern coasts of the three continents but to discuss their effects relative to areas at similar latitudes with differing currents, eastern shores at the same latitudes are mentioned more briefly.

The marine biota of the southern oceans is poorly known relative to that of the northern hemisphere. Discussion of faunal distributions must therefore be circumspect. The concept of biogeographic provinces or zones remains a somewhat contentious one and indeed there is no quantitative definition of a province that has enjoyed general support. The broader principles of marine zoogeography have been discussed by many workers, foremost amongst them Ekman (1953) and Briggs (1974). In concentrating on the effects of the major currents, this paper is a simplified discussion of zoogeography in the three systems. Ambient hydrographic conditions including currents are by no means the only determinants of marine faunal occurrences. In particular, geological and long term climatological events associated with the movement of continents have had major influence upon the distributions and affinities of modern faunas. Present conditions, especially currents, act as recent

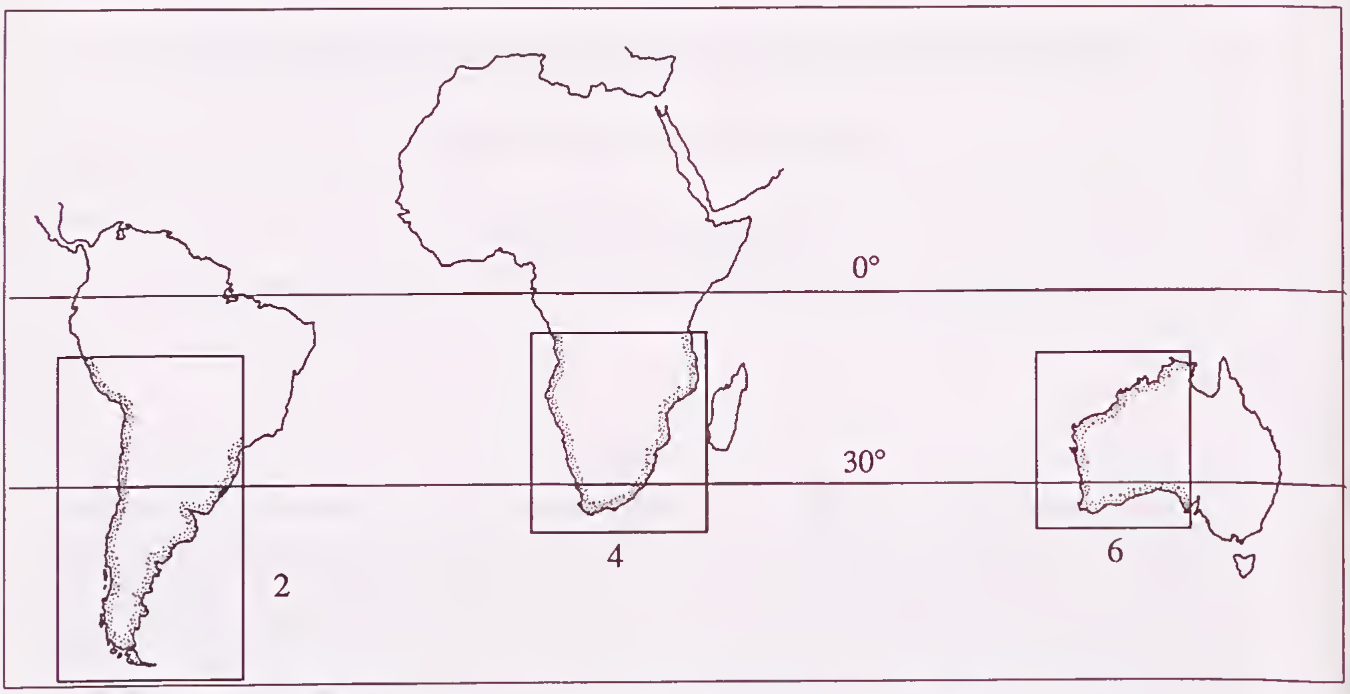

Figure 1 Regions discussed in this paper. Inserts enlarged in figures 2, 4 and 6.

modifiers of those longer term processes. The provinces here discussed are taken from the recent literature.

We have attempted to incorporate data on a wide variety of taxa but our personal interests result in a bias towards crustaceans and molluscs. The Humboldt, Benguela and Leeuwin Currents are surface currents and have limited direct influence on deeper waters. As such, this discussion is restricted to faunas of the intertidal and subtidal zones to about 200m depth.

South America

Currents: Extending south to 56°S, the western coast of Peru and Chile is contacted directly by the West Wind Drift that splits into the northward flowing Peru, or Humboldt, Coastal Current and the southward flowing Cape Horn Current that skirts the Cabo de Hornos and flows northward along the east coast as the Falkland Current (Fig.2). The Humboldt Current usually contacts the west coast at 41-46°S but in winter it may develop as far north as 32°S. The northward progression of this current and the prevailing southwesterly winds result in major upwellings of cool waters to the surface along most of the central and northern Chile coast.

In apposition to the Humboldt Current, warmer subtropical water is transferred south by the surface Chile Coastal Counter-current. The southern penetration of this current usually reaches to 37°S in summer and only 31°S in winter. At the Subtropical Convergence (23-25°S in winter, 33-34°S in summer), the Humboldt Current flows under this warmer water.

The net effect of water current movements is that there are relatively small differences in water temperatures over large distances of the Chile-Peru coastline (Brattström & Johanssen 1983).

Provinces: The relatively constant hydrographic conditions along the coast of southwestern South America (Brattström & Johanssen 1983, Brattstrøm 1990) suggest that biotic distributions should show

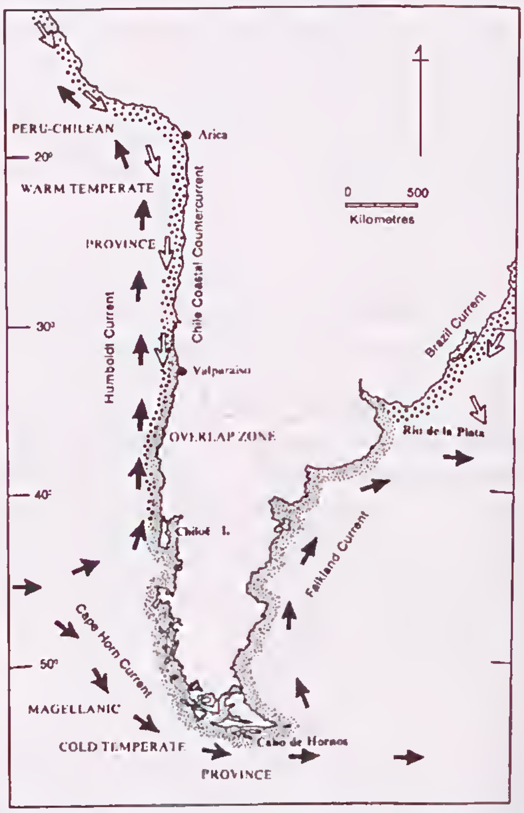

Figure 2 Zoogeographic provinces of southwestern South America. Cold currents indicated by solid arrows, warm currents by open arrows. (After various authors especially Briggs 1974, Brattström & Johanssen 1983).

clinal rather than sudden changes in composition. Indeed, most intertidal and shallow-water species have very large ranges along this coast (Brattström 1990). However, the distribution patterns for many taxa support the recognition of two zoogeographic provinces, one cold temperate (or antiboreal), the other warm temperate (Fig. 3).

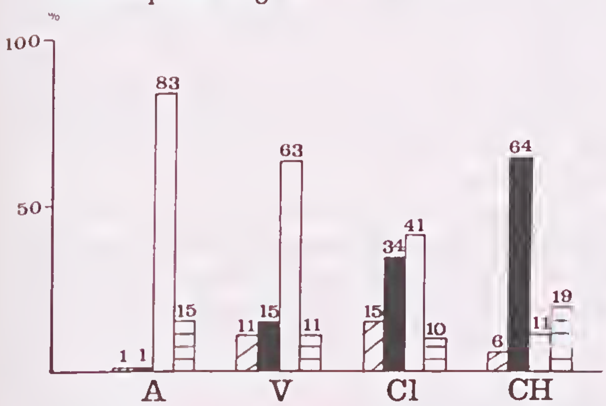

Figure 3 Composition of fauna (mixed taxa) along southwestern coast of South America. ▨: endemic species; ■ :species with southern affinities; □ :species with northern affinities; ⊟ :other. A: Arica; V: Valparaiso; Cl: Chiloé Island; CH: Cabo de Hornos. (Calculated from data of Brattström & Johanssen 1983).

South of about 42°S, the northern end of Chiloé Island, the faunal assemblages show cold temperate affinities and this province is usually known as the Patagonian or Magellanic Province. Its northern border corresponds closely with the position of impact of the Humboldt Current on the South American coast. It is recognised that the southeastern coast of South America is also cold temperate but there is some uncertainty whether or not the southeastern and southwestern coasts should be regarded as a single or as two provinces, separated at the Cabo de Hornos.

The warm temperate province, known variously as the Peruvian, Peruvian-Chilean or Peru-Chilean Province, is recognised as extending from 2-6°S south to somewhere between 30° and 42°S. The close approach of this province to the equator is a result of the upwellings and movement of cold water by the Humboldt Current.

The southern boundary of the Peru-Chilean Province is open to some interpretation. There seems little doubt that a change in faunal composition occurs at or near 42°S, evident in the distributions of decapod crustaceans (Rathbun 1910, Haig 1955, Garth 1957), echinoderms (Madsen 1956, Bernasconi 1964), polychaetes and ostracod crustaceans (Hartmann-Schröder & Hartmann 1962), molluscs (Dall 1909, Stuardo 1964, Dell 1971, Marincovich 1973), fish (Norman 1937, Mann 1954) and mixed taxa (Semenov 1977, Brattström & Johanssen 1983). From the study of Brattström & Johanssen (1983), approximately 25% of shelf benthic invertebrates have their northern or southern boundaries at or very near 42°S.

In addition to the effects of currents at this point, the topography of the coast north and south varies. North of 42°S there are no archipelagos, few islands or sheltered bays and the rocky and sandy beaches are exposed to the open ocean. South of 42°S, the coast is fringed by archipelagos of thousands of islands, is split by narrow sounds and fjords and has more sheltered beaches and mudflats.

Most workers have acknowledged a biogeographic transitional zone extending from 42°S to somewhere between 38 and 30°S (see Brattström & Johanssen 1983: fig.18). Many cold temperate species from the Magellanic Province extend into the Peru-Chilean, though few reach farther north than 30°S. This southern component is replenished by dispersals in the cold water of the northward flowing Humboldt Coastal Current. Most species in this region, however, are warm temperate. Some workers have regarded the transition zone as a separate province (*eg* Knox 1960: Central Chilean Province) but most agree with Dahl's (1960) observation that characterization of a province by a strong endemic element is lacking. Brattström & Johanssen (1983) argued that the transitional area, having a preponderance of warm temperate species, is part of the Peru-Chilean Province. It could also be suggested that it is an overlap zone of the two provinces, similar to that proposed for western Australia. Balech (1954) and Brattström & Johanssen (1983) attributed the transitional zone to variations in the relative effects of the cold Humboldt Current and warmer Chile Coastal Counter-current. There is little variation in hydrographic conditions south of 42°S.

The proportion of endemic faunas varies considerably between taxa. For the warm temperate Peru-Chilean Province, endemicity of 23-53% has been recorded for littoral molluscs (Dall 1909) and decapod crustaceans (Haig 1955, Garth 1957) and Briggs (1974) suggested that at least 50% of fish may be endemics. For the cold temperate Magellanic Province, including both southwestern and southeastern coasts, endemicity figures are generally higher with estimates of 33-61% for anomuran and isopod crustaceans, echinoderms, bivalve molluscs and fish (Ekman 1953, Haig 1955, Madsen 1956, Soot-Ryen 1959, Menzies 1962, Pawson 1969, Briggs 1974).

As was noted above, there is some uncertainty as to the southern boundary of the Magellanic Province. Stuardo (1964) suggested that Cabo de Hornos might be regarded as a boundary between two cold temperate provinces. Other authors have suggested several cold temperate provinces for South America, either with a border at Cabo de Hornos (Balech 1954) or with the southernmost landmass of the continent on both sides of the Cabo de Hornos in one province and a further cold temperate province adjoining to both the east and west (Forbes 1856, Knox 1960). Most authors have treated the southwestern and southeastern coastline as belonging within a single province (Briggs 1974) although the southeastern fauna is much less well known. The northern boundary of this province on the east coast is generally regarded as coinciding with the Rio de la Plata at 35°S where the cold Falkland Current diverts to the east as it contacts the warm Brazil Current. An Eastern South American Warm Temperate Province is recognisable from 35°S to approximately Cabo Frio at 23°S but the composition of this fauna is very poorly known (Briggs 1974).

Summary: The major provincial boundary of cold temperate faunas of southwestern South America coincides with the normal point of impact of the Humboldt Current. This current flows north, dispersing cold water and southern species while the Cape Horn Current flows south. The point of divergence of currents acts as a fairly effective barrier to dispersal of inshore species. The contrasting effects of the Humboldt Current and Chile Coastal Counter-current result in an overlap zone between cold and warm temperate provinces between 30° and 40°S. The Humboldt Current extends the warm temperate conditions much farther north on the western coast (approximately 3°S) than the Falkland Current does in the east (about 23°S) (Fig.2). Thus tropical faunas range much farther south along the eastern coast than along the western.

Southern Africa

Currents: At about 35°S, the southern tip of Africa at Cape Agulhas is 20° farther north than Cabo de Hornos of South America. Nevertheless, it is affected by the cold water northward flowing Benguela Current (Fig.4). The Benguela Current and the prevailing southeast trade winds result in major upwellings along the southwest coast bringing cold sub-surface waters from 100-300 m to the surface. The Benguela Current flows northward into the Gulf of Guinea, where it encounters the warm Angola Current flowing southeastward, and then continues near the Equator as the now warm South Equatorial Current. The combined effects of the cold northward flowing current and upwellings result in relatively little seasonal variation in sea surface temperatures along the southwestern coast of Africa.

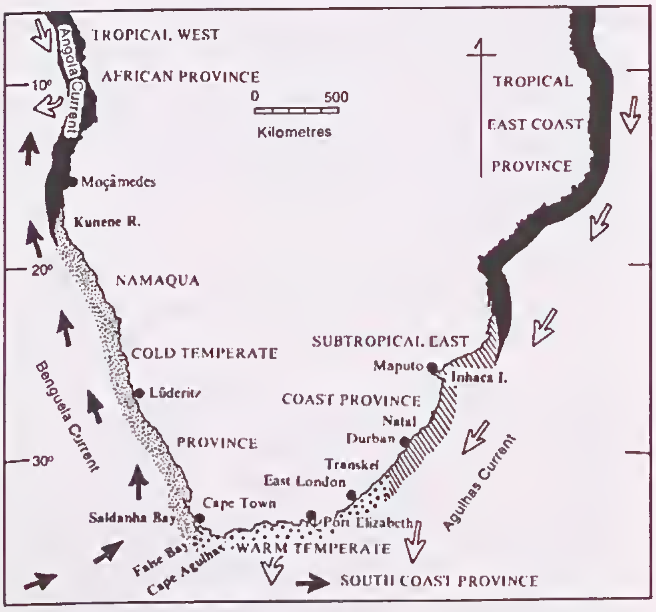

Figure 4 Zoogeographic provinces of southern Africa. Currents as per Fig. 2. (After Brown & Jarman 1978, Kensley 1981).

In contrast, the eastern coast of southern Africa is dominated by southward flowing offshoots of the Indian Ocean South Equatorial Current. The warm water Agulhas Current flows southward along the southeastern coast to the vicinity of Cape Agulhas. Some warm water moves west around the Cape but most diverts to the south on contact with the Benguela Current.

Provinces: There is a substantial literature relating to the faunal provinces of southern Africa (Briggs 1974, Brown & Jarman 1978). Early workers (Forbes 1856, Woodward 1856, Ortmann 1896) suggested that a single province extends from Angola or South West Africa (Namibia) to the vicinity of Durban. Ekman (1935) regarded this province as warm temperate. Stephenson (1947), Hedgpeth (1957) and Knox (1960) divided the coast into a cold temperate province extending from the tropics of west Africa to Cape Town and a warm temperate province east of Cape Town and best developed between Cape Agulhas and Port Elizabeth. Ekman (1953) and Briggs (1974) regarded the southwestern province as a second warm temperate one; Briggs discussed the Southwestern Africa Province from Moçamedes, Angola (15°S) to Cape Peninsula (34°S) and the Agulhas Province from Cape Peninsula east to Port Elizabeth (34°S). Briggs cited the level of endemicity of the Southwestern Province to be considerably lower than that of the Agulhas Province with figures of 17% and 34% respectively (taken from Ekman (1953), based upon Stephenson's works).

More recent papers (Brown & Jarman 1978, Kensley 1981, 1983, Kilburn & Rippey 1982) supported the existence of both warm and cold temperate provinces, with a subtropical province on the east coast north of East London. The names and precise boundaries of the provinces differ between workers, the latter at least in part due to differences in distributions between taxa. For the purposes of this discussion, the provinces of Brown & Jarman (1978) and Kensley (1981, 1983) generally will be followed (Fig. 4). This pattern differs slightly from that of Kilburn & Rippey (1982) and where significant, differences are discussed.

The Tropical West African Province extends south to 20°S although Kilburn & Rippey (1982) placed its southern limit at 17°S. The fauna of Namibia is poorly known and definition of provincial borders remains speculative. The southern limit is determined by cold water effects of the Benguela Current and upwellings and typical tropical species rarely range south of this limit (Kensley 1981). Although it may be regarded as a tropical province, the influence of the Benguela Current continues a considerable distance farther north. For example, no coral reefs occur south of the equator on the west coast, the southernmost reefs being those of the Gulf of Guinea at 0-5°N. In contrast, on the east coast coral reefs are found as far south as southern Moçambique at about 28°S.

The Cold Temperate West Coast or Namaqua Province extends from 20°S to Cape Agulhas (35°S). Kilburn & Rippey (1982) recognised an overlap zone between the Namaqua and West African Provinces, extending for 7° of latitude south of 17°S and offsetting the northern boundary of the Namaqua Province proper southwards by 4° to 24°S. The dominant influences in the province are the cold water effects of the Benguela Current and upwellings. The faunas here are more poorly known than are those to the east but are characterised by low species diversities but high populations of species present (*eg* crustaceans: Kensley 1981, 1983, molluscs: Kilburn & Rippey 1982). Productivity is high due to the nutrients brought to the surface in the upwellings. The fauna comprises few Indo-West Pacific (IWP) species and these are largely confined to the southernmost areas of the province (Kensley 1981, 1983). Atlantic-Mediterranean species proportionally dominate IWP forms amongst crustaceans and molluscs. Interestingly, the number of Atlantic crustacean species is lower in the Namaqua Province, itself situated in the South Atlantic, than in the Warm Temperate South Coast Province. The low number of Atlantic species in the Namaqua Province can be explained in terms of the water temperature regime. Water temperatures are on average warmer both north and south of the major area of upwelling at 25-30°S. The cold water of the upwellings and the northward flow of the Benguela Current act as a cold water barrier to colonisation by the more diverse tropical Atlantic faunas. Endemic species are the dominant faunal element amongst molluscs, accounting for 88% of the Namaqua species (Kilburn & Rippey 1982). Their data were pertinent only to south of the Orange River, information being too limited to speculate on endemicity farther north. The species tend not to be confined to the Namaqua Province but are endemic to southern Africa. Analysis of Kensley's (1983) data reveals that for crustaceans the endemicity is lower with 35-57% for decapods and 41-85% for peracarids, endemicity decreasing to the north. Ekman (1953) noted 17% endemicity for several taxa on the basis of Stephenson's works. Endemic fishes appear to comprise less than 20% of the fauna (Penrith 1969, Smith 1949, 1960, Briggs 1974).

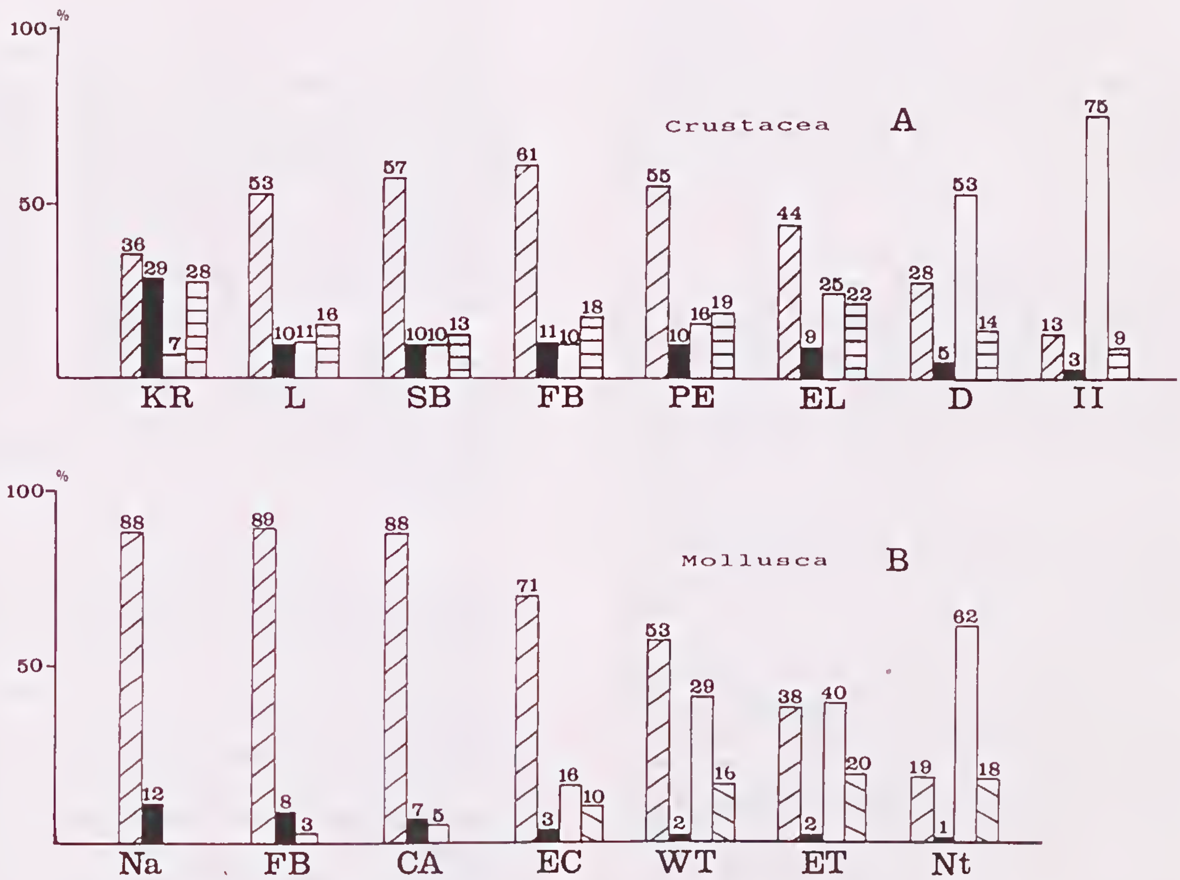

Figure 5 Composition of crustacean and molluscan taxa along southern coast of Africa.
A, Crustacea (Decapoda, Amphipoda, Isopoda combined). ▨:endemic species; ■ Atlantic-Mediterranean species; □:Indo-West Pacific species; ▤:other. KR: Kunene River; L: Lüderitz; SB: Saldanha Bay; FB: False Bay; PE: Port Elizabeth; EL: East London; D: Durban; II: Inhaca Island. (Data from Kensley 1981, 1983); B, Mollusca. As per Fig. 5A except ▨:Cape Endemics and ▧ subtropical endemics. Na: Namaqua (southern); FB: False Bay; CA: Cape Agulhas; EC: East Cape; WT: West Transkei; ET: East Transkei; Nt: Natal. (Data from Kilburn & Rippey 1983).

A south coast warm temperate province has been recognised by most workers (Briggs 1974). The Warm Temperate South Coast Province of Brown & Jarman (1978), or Algoa Province of Kilburn & Rippey (1982), extends in an east-north-east direction from an overlap zone between Cape Town to Cape Agulhas to just north of East London. Species diversity and, not surprisingly, the number of IWP species is higher than in the Namaqua Province. For peracarid crustaceans, this province is the most diverse in southern Africa. The proportion of IWP molluscs decreases progressively from east to west, reaching their western limits at False Bay/Cape of Good Hope (Kilburn & Rippey 1982) (Fig.5).

The numbers of Atlantic species are as high as or higher than in the Namaqua and as proportions of the total number of species, Atlantic representation can be as high or only slightly lower. The increase in Atlantic species to the east of Cape Agulhas, at least in the Crustacea, may be explained by at least two processes. Some species may represent relict populations of more diverse faunas present in the warmer Pleistocene Period. Others are likely to be more recent migrants, distributed by some movement of South Atlantic waters around Cape Agulhas (Shannon 1966) or by the large gyre circulation of Atlantic water into the South Equatorial Current of the Indian Ocean and thence southwest into the Agulhas Current. The warmer conditions of the Warm Temperate South Coast Province are more suitable for recruitment of many Atlantic species. The number of species endemic to southern Africa is very high. Endemics account for 33-54% of decapod and amphipod crustaceans, 88-92% of isopod crustaceans and 38-70% of molluscs (Kensley 1981, 1983, Kilburn & Rippey 1982, Gosliner 1987), with the proportion of endemics generally decreasing to the east. High endemicity has also been recorded in this province for hydroids (Millard 1978), soft corals (Williams 1990), ascidians (Millar 1962), fishes (Smith 1949, 1960, Penrith 1969) and mixed taxa (Ekman 1953, Day *et al*. 1970). Day (1978) and Kensley (1983) suggested that the province has been a centre of evolutionary radiation for crustacean groups with ancestral stock from both Atlantic and IWP origins; Millard (1978) proposed a similar evolutionary centre for hydroids.

The Subtropical East Coast Province extends from an area of overlap with the Warm Temperate South Coast Province to Inhambane, Moçambique, close to the Tropic of Capricorn. Kilburn & Rippey's (1982) equivalent Natal Province has its northern boundary 6° farther south, their interpretation being that mollusc faunas north of 29°S are essentially tropical. Coral reefs appear about midway along the north-south extent of this province indicating the warm water effects of the Agulhas Current. The diversity of decapod crustaceans increases markedly but that of peracarid groups declines (Kensley 1983). The IWP and Atlantic faunal elements continue to increase and decrease respectively in both numbers of species and proportion of total species. Endemicity declines towards the north in numbers of species and proportionally for crustaceans (Kensley 1981, 1983) and molluscs (Kilburn & Rippey 1982, Gosliner 1987) (Fig. 5). In molluscs, the endemics show a shift towards tropical rather than temperate affinities. This province may also be regarded as an overlap or transition zone between tropical and warm temperate provinces (see concluding comparison of systems).

The Tropical East Coast Province ranges from the Tropic to north of the equator; Kilburn & Rippey's (1982) Indo-Pacific Province begins 6° farther south. The province is heavily dominated by IWP forms. There are very few Atlantic and few endemic species.

Overall affinities of the fauna for the African coastline south of 15°S vary somewhat between taxa. The IWP faunal element is dominant in species diversity for decapod crustaceans (61-66% of species) (Kensley 1981, 1983) while the Cape endemic component is dominant for peracarid crustaceans (46% of amphipod species, 65% of isopod species) and molluscs (19-89%, depending on locality, Kilburn & Rippey 1982) (Fig.5). The Atlantic-Mediterranean element accounts for only 5-15% of crustacean and 1-12% of molluscan species.

Summary: The Benguela Current affects the distribution of inshore faunas in several ways. It circulates cold water northwards and encourages the upwellings of sub-surface water along the southwestern coast. The current and upwellings combine to extend a cold temperate province to within 20° of the equator and form an effective cold water barrier to movement of warm water Atlantic species southwards and to warm water IWP species westwards. There is a distinct containment of tropical faunas to the north of the cold water province. The western coast tropical province has its southern boundary at least 5° farther north than its equivalent province on the eastern coast. Areas on the eastern coast at similar latitudes to that of the cold temperate Namaqua Province are subtropical or warm temperate.

Southwestern Australia

Currents: The southwestern coast of Australia extends just south of 35°S near Albany, similar in latitude to the southern tip of Africa and is therefore north of the main flow of the West Wind Drift. The southward flowing Leeuwin Current, originating to the north of North West Cape (21° 47'S), brings warm, low salinity water south around Cape Leeuwin and east into the Great Australian Bight (Cresswell & Golding 1980, Godfrey & Ridgeway 1984, Pearce & Cresswell 1985, Pearce 1991) (Fig.6). The Leeuwin Current usually peaks in the winter, becoming weak in summer. It flows along the outer continental margin off the coast, intercepting offshore islands but not the inshore continental coastline until the Cape Naturaliste-Cape Leeuwin area. Because of the Leeuwin Current there is no substantial upwelling along the southwestern coast of

Figure 6 Zoogeographic provinces of Western Australia. Currents as per Fig. 2. (After Wilson & Allen 1987).

Australia. Surface waters are nutrient poor and primary productivity is low.

The Leeuwin Current roughly parallels the East Australian Current that brings warm waters southward to about 33°S before diverting as eddies into the Tasman Sea. Thus, unlike South America and Africa, Australia has southward flowing warm currents on both western and eastern coasts.

Provinces: Biogeographic reviews of Australian marine inshore fauna, especially intertidal species, from the 1930's into the 1970's recognised five to six provinces, of which two occurred along the western coast (Whitley 1932, Bennett & Pope 1953, Knox 1963, Briggs 1974). A tropical province, the Dampieran, extended from about Shark Bay or Geraldton north and east to Cape York and a warm temperate province, the Flindersian, extended from the Dampieran south and east to western Victoria.

More recently, the marine biogeographic zonation of Australia has been simplified into a recognition of a Northern Australian Tropical and a Southern Australian Warm Temperate Province with broad zones of overlap on both western and eastern coasts that for this discussion will be regarded as the Western Coast and Eastern Coast Overlap Zones (Fig.6) (Wilson & Gillett 1971, Marsh 1976, Wilson & Stevenson 1977, Wells 1980, 1986, 1990, Wilson & Allen 1987).

The northern coast of Western Australia, northeast from North West Cape, has a tropical biota that is continuous with other parts of the Indo-West Pacific. In general, species diversity decreases with increasing latitude but there are no major distributional boundaries, most species reaching as far south as North West Cape. Endemicity is low in the Northern Australian Tropical Province with about 10% of mollusc species (Wilson & Allen 1987), 13% of fishes (Wilson & Allen 1987), 17-22% of brachyuran and anomuran decapod species (Griffin & Yaldwyn 1967, Morgan 1990), essentially no corals (Potts 1985, Veron 1985, Wilson & Allen 1987) and, for the northwestern coast, about 13% of echinoderms (Marsh 1976, Marsh & Marshall 1983) being endemic to Australia (Fig.7). The relationship of the tropical northern coast with other parts of the Indo-West Pacific has been most recently discussed by Wells (1986, 1990) and Wilson & Allen (1987).

The southern coast of Western Australia east of Cape Leeuwin (34°22'S) is part of the Southern Australian Warm Temperate Province. In addition to the effects of the weakening Leeuwin Current, the warm temperate province is influenced by the cold West Wind Drift, which has been responsible for the distribution of some widespread or circumpolar elements into the southern Australian fauna (Fell 1962, Knox 1979, Edgar 1986). IWP species representation is low and decreases from west to east. Most of the temperate species that occur along the south coast of Western Australia reach as far west as Cape Leeuwin without major biogeographic discontinuities. Rates of species endemicity are much higher in this province than in northern waters: approximately 85% for fishes (Wilson & Allen 1987), possibly 95% for molluscs (Wells 1980, Wilson & Allen 1987), 90% for echinoderms (Clark 1946, Rowe & Vail 1982) and 63% for decapod crustaceans (77% endemic to Australia) (Morgan & Jones 1991).

Fig. 7 shows the affinities of crustaceans and molluscs of western Australia. Note that for crustaceans, species endemic to Australia are plotted, accounting for a high proportion of the south coast fauna. For molluscs, south coast endemics are incorporated in the category of species with southern affinities and endemics are those confined to the four regions.

In many respects, the Western Coast Overlap Zone is a region of transition with gradual replacement of a tropical fauna in the north by a predominantly temperate fauna in the south (Wilson & Allen 1987). There is a small proportion of species endemic to Western Australia and most of these have at least part of their range in the Western Coast Zone and often achieve their greatest numbers there (Wells 1980, Wilson & Allen 1987). The proportion of endemics varies between taxa: 20% for shallow water asteroids (Marsh 1976) and less than 10% for prosobranch molluscs (Wells 1980).

Two offshore regions clearly illustrate the effects of the Leeuwin Current on faunal composition: the Houtman Abrolhos (28-29°S) and Rottnest Island (32°S).

Although it has substantial numbers of temperate species and Western Australian endemics, the fauna of the Houtman Abrolhos is essentially tropical (Montgomery 1931, Wilson & Marsh 1979, Wells 1980, Veron 1985) and the Abrolhos is generally considered to be the southern limit in Western Australia of the tropical marine biota (Wells 1980, Wilson & Allen 1987). The southern limit of the tropical fauna in eastern Australia is usually regarded as being slightly farther north, somewhere between 26° and 27°S (Endean 1957, Wilson & Gillett 1971).

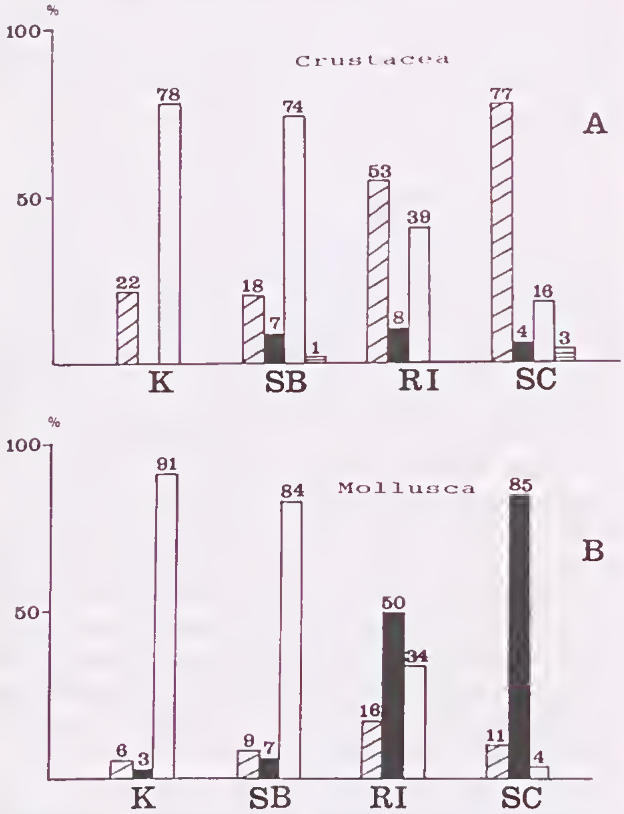

Figure 7 Composition of crustacean and molluscan taxa along western coast of Australia.
A, Crustacea (decapods only except Rottnest Island). ▨:Australian endemic species; ■:species with southern affinities (excluding south coast endemics); □:Indo-West Pacific species; ▤:other. K: Kimberleys; SB: Shark Bay; RI: Rottnest Island; SC: South Coast. (Data from Jones 1990; Morgan 1990, Morgan & Jones 1991.)
B, Mollusca. :▨ species endemic to the region, ■:species with southern affinities (including Australian south coast endemics); □:IWP species. (Data in part from Wells 1980)

Hodgkin *et al.* (1959) recorded 18 tropical invertebrate species at Rottnest Island. Hutchins (1979) found that about 26% of the 350 fish species recorded from Rottnest Island were of tropical origin and almost 40% of marine crustaceans known from the island are tropical IWP species (Jones & Morgan unpublished data) (Fig.7). The coral *Pocillopora damicornis* forms a small reef near Parker Point, the southernmost reef development in the state and one of the most southerly in the world. The fauna associated with the coral is similar to that of many tropical localities elsewhere in the world (Black & Prince 1983). The tropical *Echinometra mathaei*, the dominant echinoid at the western end of Rottnest Island, shows a continuous reproductive season typical of tropical species (Pearse & Phillips 1968). Black & Johnson (1983) reported that many of the fauna at Rottnest Island are of tropical origin.

Tropical marine invertebrates extend farther to the south, well into the Southern Australian Temperate Province. Maxwell & Cresswell (1981) have shown that larvae of tropical species can be distributed into the Great Australian Bight by the Leeuwin Current. Wells (1980) showed that 9 of 308 tropical prosobranch gastropod species examined reached Cape Leeuwin and 5 extended onto the south coast. Veron & Marsh (1988) found that 25 of 318 species of hermatypic corals reached as far south as Rottnest Island and 9 species occurred on the south coast.

Differences in composition of the fauna between inshore and offshore areas have long been known (Saville-Kent 1897, Dakin 1919). Wells (1985) found that proportions of tropical, temperate and endemic molluscs were almost identical at the eastern end of Rottnest and inshore. The proportion of endemic species at the western end of Rottnest was similar (13-16%) but the proportion of tropical species was nearly double and temperate species declined from 67% inshore and at the eastern end of Rottnest to 52% at the western end. Similarly, molluscan biomass and densities were dominated by temperate species at inshore sites while tropical species accounted for over half the biomass and density at some western end sites.

Summary: The warm southward flowing Leeuwin Current disperses tropical representatives of many taxa to the southwestern and southern coasts of Australia. No cold temperate province exists and tropical and warm temperate provinces grade into each other in a broad overlap zone. The offshore nature of the current results in higher proportions of tropical marine faunas at offshore localities than along the mainland. Due largely to the effects of the Leeuwin and East Australian Currents, the pattern of provinces is similar along the western and eastern coasts of Australia.

Comparison of Humboldt, Benguela and Leeuwin Systems

There are substantial differences between the hydrography and marine faunas of the southwestern coasts of South America, Africa and Australia. Although South America reaches fully 20° of latitude farther south than Africa and southwestern Australia, there are greater similarities in inshore water circulation between South America and southern Africa. Both show a general pattern of northward moving cool waters along their western coasts that is reinforced by a series of major upwellings. In contrast, the southwestern coast of Australia lacks both a northward flowing cold current and significant upwellings. The dominant inshore current is southward flowing and warm water. Australia is unique amongst the mid-latitude southern continents in having a similar pattern of major currents on western and eastern coasts.

The Humboldt and Benguela Currents serve to extend temperate waters and their associated faunas much farther north than along the Western Australian coast. In South America, a warm temperate province extends north to about 3°S and in southern Africa, a cold temperate province to within 20°S. The cold waters and northward flow serve as effective barriers to southward movement of tropical west coast faunas that are restricted to only limited penetration south of the equator. The cold water conditions also restrict invasion by eastern coast tropical and warm water species, distributed much farther southward than on the respective western coasts. The Humboldt and Benguela Currents therefore act as barriers to warm water species through distributional and environmental effects.

The Leeuwin Current extends warm waters much farther south along the southwestern Australian coast. A tropical north coast province extends to about 22°S inshore and to 29°S at the Houtman Abrolhos, approximately 19° (26°) and 2° (9°) farther south than in western South America and southern Africa respectively. Many tropical species with IWP affinities are distributed southward with a significant tropical inshore faunal element evident as far south as Rottnest Island at 32°S. A number of tropical species range farther south into the Great Australian Bight. There is no distinct barrier to warm water species, tropical faunas instead gradually diminishing with increasing latitude. Coral reefs are richly developed at the Houtman Abrolhos and occur at Rottnest Island but are found no farther south than 1°28'S and 0-5°N off southwestern South America and Africa respectively (Kensley 1981, Wells 1988).

A comparison of the marine zoogeographic provinces of the three continents reveals some close similarities between the western coast of Australia and the eastern coast of southern Africa. The Northern Australian Tropical Province and the Tropical East Coast Province of Africa share high species diversity, a high incidence of tropical IWP species and low species endemicity. The Western Coast Overlap Zone of Australia and the Subtropical East Coast Province of Africa have relatively high but decreasing diversity, many IWP species and a recognisable endemic component. The Southern Australian Warm Temperate Province and the Warm Temperate South Coast Province of Africa show decreased diversity, fewer tropical species that diminish with increasing latitude and relatively high numbers of endemics. For many taxa, these provinces appear to have the highest rate of endemicity in western Australia and southern Africa and in the latter region has the highest diversity for some groups (*eg* peracarid crustaceans).

It is more difficult to make valid comparisons between western Australian and eastern South American provinces. The marine fauna of the latter region remains very inadequately described. The Brazilian Province shows high species diversity and low endemicity, broadly similar to the Australian Tropical Province. There is no recognised overlap zone between tropical and temperate provinces of eastern South America but this may reflect more the paucity of faunal distributional data rather than a real disjunction between provinces.

There is no southwestern Australian counterpart to the cold temperate Magellanic and Namaqua Provinces of southern South America and southwestern Africa. Consequently there is no corresponding drop in diversity, rise in productivity and retreat of tropical faunal elements associated with a cold water mass and upwellings. There is no distinct cold water barrier to dispersal and recruitment of tropical species.

Largely as a result of inshore circulation effects, the marine biogeographic provinces of the western and eastern coasts of South America and Africa are asymmetrical. This is particularly true for southern Africa where the cold temperate province is offset to the southwest. In Australia, the pattern of provinces is essentially symmetrical along the western and eastern coasts with relatively minor differences in the extent of provinces due to variable effects of the Leeuwin and East Australian Currents.

It is wise to conclude this review with the note of caution sounded in the Introduction. Prevailing hydrographic conditions are modifiers of faunal distributions established by long term geological and climatological processes. This can be illustrated briefly for Australia. Throughout the mid- to late Tertiary, the southwestern coast supported a high proportion of faunas originating in the late Mesozoic tropical ocean Tethys and derived IWP species. This is in contrast to southeastern Australia which then had many temperate palaeoaustral forms (Knox 1980, Darragh 1985, Wilson & Allen 1987). Most invasions of tropical species along the southern Australian coast have been from the west. The present hydrographic conditions have maintained rather than caused the relatively high tropical influence in southwestern Australia.

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